

NEOSELACHIAN SHARKS' TEETH FROM THE LOWER CARBONIFEROUS OF BRITAIN AND THE LOWER PERMIAN OF THE U.S.A.

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ABSTRACT. Isolated teeth of *Anachronistes fordi* gen. et sp. nov. are recorded from the Upper Carboniferous Limestone, Lower Carboniferous of Derbyshire, England, and Clwyd, North Wales. The teeth are assigned to the Family Anachronistidae fam. nov. of uncertain position within the neoselachian sharks. A further unnamed tooth belonging to the genus is recorded from the Lower Permian of Nevada, U.S.A. The teeth of *Anachronistes* are neoselachian since they possess a conical central cusp, well-developed lateral blades and basal flange, V-shaped basal root face and hemiaulacorhize vascularization. The teeth of *Anachronistes* lack enameloid. The teeth are most closely comparable to those of *Squatina* and *Orectolobus*, and belong to a bottom feeder. The teeth extend the record of the neoselachian sharks from the Lower Norian (Upper Triassic) back into the Dinantian (Lower Carboniferous). Two types of monognathic gradient heterodonty are distinguished: linear gradient heterodonty in which there is gradual reduction in coronal profile commissurally; and non-linear gradient heterodonty, where coronal profile reduction occurs both mesially and distally from a central high tooth row.

SHARK remains are known from deposits of Lower Devonian to Recent age. Articulated skeletons are rare in the fossil record, with the exception of certain lithologies, such as black and oil shales (for example, the Lower Carboniferous shales of Mazon Creek in Illinois, U.S.A., the Lower Carboniferous of Glencartholm, Scotland, and the Lower Jurassic of north-west Europe) and very fine-grained limestones (for example, the Upper Jurassic of the Solnhofen-Eichstätt area in southern Germany, the Upper Cretaceous of the Hakel and Hajula regions of the Lebanon, and the Monte Bolca limestone from the Italian Eocene).

More commonly, fossil shark remains comprise the isolated mineralized hard parts of the skeleton (Applegate 1967). Of these, teeth, dorsal fin spines, and dermal denticles are the most common, although calcified vertebrae, jaw cartilages, and occasional specialized dermal structures such as clasper spines and cephalic spines are also known. From the point of view of shark taxonomy, teeth, dorsal fin spines, and calcified vertebrae have proved the most useful, and are the most intensively studied.

Three successive levels of organization were recognized by Schaeffer (1967) in living and fossil sharks. These were designated the cladodont, hybodont, and modern shark levels. Various authors have since incorporated Schaeffer's levels of organization into a taxonomic framework for the sharks (Blot 1969; Compagno 1973, 1977; Maisey 1975; Duffin 1980). There are now generally taken to be four cohorts within the Elasmobranchii: the cladodontiforms which include cladoselachians, various cladodont groups, and xenacanth; the hybodontiforms which include the hybodonts, tristychiids, and related genera; the ctenacanthiforms which include the ctenacanthids; the neoselachiforms which include all living sharks and rays plus the palaeospinacids, orthacodontids, and anacoracids.

The definition of the neoselachian condition is based mainly upon skeletal characters (Compagno 1973, 1977; Reif 1977), amongst the most important of which are the possession of calcified vertebrae, subterminal hyostylic jaws, U-shaped scapulocoracoid, and only one or two basal segments between the enlarged pelvic basipterygium and the clasper shaft cartilage in adult males. Dorsal fin spines, when present, lack posterior ornament, and possess an at least partly lamellar trunk which meets the mantle at a sharply defined junction (Maisey 1975).

There has been some debate over the recognition of neoselachian teeth (see Duffin 1981 for a review). Reif (1973, 1977, 1978, 1980) prefers the use of enameloid ultrastructure. In most neoselachian sharks the enameloid is triple layered; a basal layer of tangled apatite fibres is overlain by a middle layer of parallel fibre bundles, which in turn is overlain by a surface layer of shiny enameloid. The teeth of ctenacanths and hybodonts possess only a single crystallite enameloid, within which the apatite crystallites are randomly oriented. Root morphology and vascularization are also important taxonomic criteria. Casier (1947a-c) concluded that whilst hybodonts and ctenacanths possess a simple root with many entrant vascular foramina of no particular spatial organization, the vascularization of neoselachian teeth is reduced, often to a single medio-internal vascular canal flanked by a series of lateral vascular canals. The basal face of the root in neoselachian sharks teeth is usually a modified V-shape (Duffin 1980).

At the present time the oldest known neoselachian shark is *Reifia minuta* Duffin (1980), which is represented by isolated teeth from the Lower Norian (Upper Triassic) of southern Germany. From this time onward, neoselachian remains occur sporadically through the stratigraphic column.

The cohort Neoselachii are divided into four suborders (Compagno 1973), all of which are represented in the Jurassic: the Squalomorphii are represented by *Squalus* in the Cretaceous (Herman 1975), hexanchoids ('*Notidamus*') in the Tithonian of southern Germany (Schweizer 1964), and possibly by *Pseudodolalotus barnstonensis* Sykes (1971) in the British Rhaetic and the Rhaetian of the Lombardy Alps (Sykes 1974; Reif 1978; Duffin 1978; Tintori 1980); the Squatinomorphii are represented by possibly four species of *Squatina* from the Tithonian of Solnhofen (Dinkel 1920; Schweizer 1964); the Batoidea are represented by *Spathobatis bugesiacus* Thiollière (1849), *Belemnobatis sismiondae* Thiollière (1854), and *Asterodermus platypterus* Agassiz (1843) from the Tithonian of Germany and France; all four families of the Galeomorphii are represented—Heterodontiformes by *Heterodontus falciifer* (Wagner 1857) from Solnhofen, Carcharhiniformes by *Palaeoscyllium formosum* Wagner (1857) from Solnhofen, Lamniformes by *Palaeocarcharias stromeri* de Beaumont (1960) from Solnhofen, and Orectolobiformes by *Crossorhinus jurasicus* Woodward (1918), *Phorcynis catulina* Thiollière (1854), and *Corysodon cerinensis* Saint-Seine (1949) from the Lower Tithonian of Solnhofen and France.

Duffin (1981) has reviewed the pre-Jurassic record of the neoselachians. There is no neoselachian known in pre-Norian deposits at the present time.

The fact that the major taxonomic categories of the neoselachian sharks were in existence during the Jurassic, and in some cases during the Upper Triassic, implies the existence of neoselachian sharks before the Upper Trias. The lack of fossil evidence of neoselachian sharks in Lower Triassic and Permian strata is probably due to the absence of suitable marine deposits. It is reasonable, therefore, to look to the Carboniferous for evidence of early neoselachian history.

The object of this paper is to describe new selachian teeth from the British Lower Carboniferous and the Permian of the U.S.A., and to discuss their affinity to the neoselachians.

METHODS

The teeth described in this paper come from three sites: Steeplehouse Quarry, Wirksworth, Derbyshire; Quarry dump at Esclusham Mountain, near Minera, Clwyd, North Wales; Ward Mountain, Pine County, Nevada, U.S.A.

The teeth from Steeplehouse Quarry were collected from bulk samples made between 1972 and 1979. Both the limestone and shale partings were sampled. The limestone was dissolved in a 5% solution of formic acid buffered with calcium orthophosphate, and yielded a rich phosphatic residue. The shale was disaggregated by repeated drying, soaking in paraffin oil (kerosene), and then further soaking in boiling water. The shale yielded a less concentrated phosphatic residue.

The Permian tooth from Ward Mountain was sorted from disaggregated residues prepared from thinly bedded limestones and calcareous sandstones for microfossil study.

The teeth from Esclusham Mountain, North Wales, were dissolved by acid preparation from four small hand specimens of limestone that displayed visible petalodont tooth plates and other vertebrate debris.

SYSTEMATIC PALAEOLOGY

Class CHONDRICHTHYES

Subclass ELASMOBRANCHII

Cohort NEOSELACHII

Superorder and Order incertae sedis

Family ANACHRONISTIDAE nov.

Familial diagnosis. Known only on the basis of small (1 to 2 mm long) isolated teeth. The crown possesses a lingually inclined central cusp. The crown base possesses well-developed lateral blades, and a basal flange is developed, underlain by a basal groove at the crown/root junction. The root possesses a downward-projecting labial buttress beneath the basal flange of the crown. A central pit is developed lingual to the labial buttress. The remainder of the root is lingually extended and moderately deep. The basal face is arcuate in basal view; the two lateral wings are directed labially. The root vascularization comprises a single median internal canal which is usually roofed by the basal face of the root. The root is hemiaulacorhizoid.

Genus ANACHRONISTES gen. nov.

Type species. *Anachronistes fordii* sp. nov.

Derivation of name. The generic name is derived from Anachronismos (Greek—out of time) and refers to the early position of these teeth in the stratigraphic record.

Generic diagnosis. As for Family.

Anachronistes fordii sp. nov.

Plate 13, figs 1–10; Plate 14, figs 1–7, 9; text-figs. 2A, 3D

Derivation of name. The specific name is dedicated to Dr. Trevor D. Ford of Leicester University, since it was his work (Ford 1964, 1980) which led us to sample the fish-bed at Steeplehouse Quarry.

Diagnosis. As for the genus.

Holotype. British Museum (Natural History), Department of Palaeontology number P.60670. An isolated, almost perfect tooth (Pl. 13, figs. 6, 7, 9, 10), from Steeplehouse Quarry, Derbyshire.

Other material. Thirty-five isolated teeth from Steeplehouse Quarry (BM(NH), P.60671, Pl. 13, fig. 1, Pl. 14, fig. 3; P.60673, Pl. 13, fig. 3, Pl. 14, figs. 5, 6; P.60674, Pl. 13, figs. 4, 5, 8; P.60675, Pl. 13, fig. 2; P.60690, Pl. 14, fig. 4; P.60697, Pl. 14, figs. 1, 2; P.60676 to P.60689, P.60691 to P.60696, and P.60698 to P.60705). One isolated tooth from Esclusham Mountain (P.60672, Pl. 14, figs. 7, 9). The teeth are very friable.

Type locality. Steeplehouse Quarry (disused), Wirksworth, Derbyshire, U.K., Grid reference SK 288554.

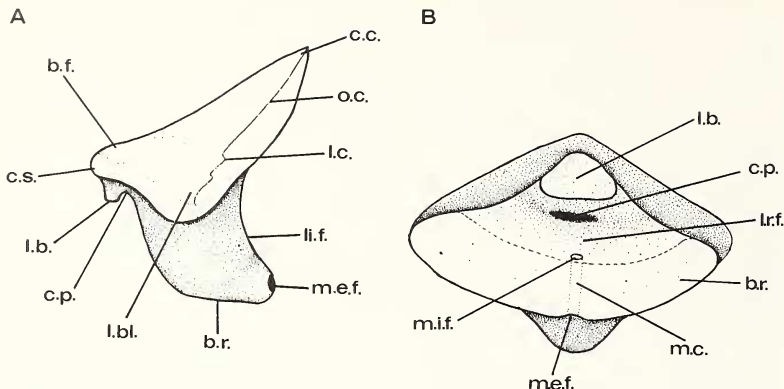
Age. Cawdor Limestones, P₁ sub-zone, Upper Viséan, Dinantian, Lower Carboniferous.

Lithology. Interbedded crinoidal limestone and black shale bands.

Other localities. Quarry tip at Esclusham Mountain, south-west of Minera, Clwyd, North Wales. Grid reference SJ 253503. The original location of the limestone debris yielding teeth of *Anachronistes* is unknown. The age of local deposits is presumed to be Asbian to Brigantian, Viséan, Dinantian, Lower Carboniferous (Dr. B. Rosen pers. comm.).

Description of the Holotype. The tooth is small, measuring 1.9 mm mesio-distally, 1.56 mm high, and 1.5 mm labio-lingually from basal flange to cusp apex. The tooth is fairly well preserved, sustains some polish due to post-mortem transport, and is cracked.

The crown is well developed, its most prominent feature being a lingually directed central cusp (c.c. in text-fig. 1, which gives a guide to the descriptive terminology used in the text). The apical angle of the central cusp is approximately 45° (Pl. 13, fig. 6). The cutting edge of the crown is formed by a moderately developed occlusal



TEXT-FIG. 1. Diagrammatic representation of a typical tooth of *Anachronistes* in A, lateral view; B, basal view, in order to show descriptive terminology. Abbreviations: b.f., basal flange; c.c., central cusp; o.c., occlusal crest; l.c., lateral cusplet; c.s., crown shoulder; l.bl., lateral blade; l.b., labial buttress of the root; c.p., central pit housing prominent vascular foramen; b.r., basal face of the root; li.f., lingual face of the root; l.r.f., labial face of the root; m.c., median vascular canal; m.i.f., medio-internal foramen; m.e.f., medio-external foramen.

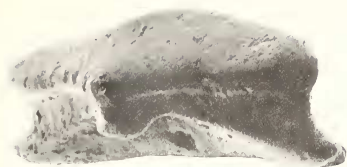
crest (o.c.) running the length of the crown mesio-distally. The occlusal crest passes through the apex of the central cusp. The central cusp is flanked on either side by a well-developed lateral blade (l.bl.) which is triangular in shape. The labial shoulder of the crown (c.s.) is substantially inflated to form a basal flange (b.f.) (Pl. 13, fig. 6). The labial face of the crown is comparatively short at the mesial and distal extremities of the crown, and is roughly rhomboidal in occlusal view (Pl. 13, fig. 9). The lingual face of the crown is moderately deep, sloping labially toward the crown/root junction. The lingual face of the crown is somewhat inflated centrally, toward the base of the central cusp. No lateral or accessory cusplets are developed. Both labial and lingual faces of the crown lack ornament. Just above the crown/root junction on the lingual face, at the base of the central cusp, there is a very small wear facet (Pl. 13, fig. 10).

The junction between the crown and the root is not well marked in this specimen. The labial basal flange of the crown substantially overlaps the crown/root junction (Pl. 13, fig. 6), whereas the crown/root transition is much smoother on the lingual side (Pl. 13, fig. 10). The mesial and distal extremities of the crown extend well beyond the crown/root junction (Pl. 13, figs. 9, 10).

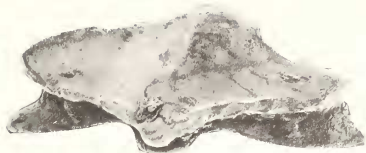
The root has a roughly triangular attachment to the crown, the longest side of this figure being the lingual root border. The labial protrusion of the basal flange of the crown over the crown/root junction gives the root the appearance of having been lingually displaced in basal view. The bulk of the root projects lingually from the crown/root junction (Pl. 13, fig. 6). On the labial side, a short (labio-lingually), labial root buttress (l.b.) base is

EXPLANATION OF PLATE 13

Figs. 1-10. *Anachronistes fordii* from the Lower Carboniferous of Derbyshire, England. 1, P.60671 in oblique labial view, $\times 30$. 2, P.60675 in labial view, $\times 35$. 3, P.60673 in lateral view showing labial flange, $\times 50$. 4, P.60674 in labial view, $\times 35$. 5, P.60674 in labio-basal view, $\times 35$. 6, P.60670 (Holotype) in lateral view, $\times 35$. 7, P.60670 in oblique lingual view, note the conical central cusp, well-developed lateral blades, and labial flange, $\times 30$. 8, P.60674 in lateral view, $\times 40$. 9, P.60670 in labial view, note the conical central cusp, well-developed lateral blades, and labial flange, $\times 35$. 10, P.60670 in lingual view, $\times 35$.



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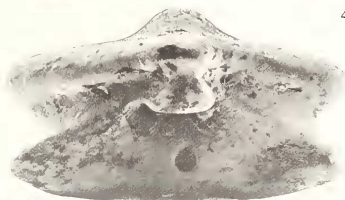
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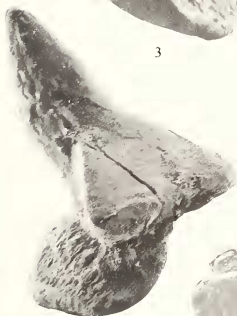
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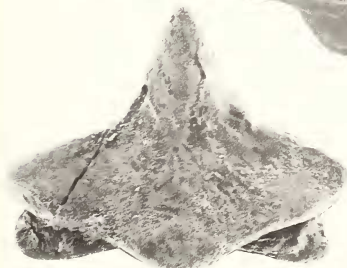
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9



10

located beneath the labial basal flange at the base of the central cusp. This labial projection of the root is non-foraminate and triangular in basal view. It is separated from the remainder of the root by a deep central pit (c.p.), which appears to expose the crown/root junction internally. From the central pit, the remainder of the labial root face descends steeply toward the basal face. Mesially and distally, the root becomes increasingly longer, such that the mesio-lateral and disto-lateral root faces converge in their ascent to the crown/root junction (Pl. 13, fig. 10). The basal face of the root is mildly arcuate and flat.

The vascularization of the root comprises a large median internal vascular canal (m.c.) situated central to the basal root face, and running labio-lingually, opening by a medio-internal foramen (m.i.f.) and medio-external foramen (m.e.f.) along the labio-basal and linguo-basal borders of the root respectively (Pl. 13, fig. 10). The medio-external foramen is accommodated in a notch on the linguo-basal border of the root.

Variation. The teeth in the sample vary from 1 to 2 mm in length (mesio-distally) (P.60695 is 2 mm long). The morphological features which are most variable within the sample, are degree of lingual inclination and distal inclination of the central cusp, prominence of the basal flange, the development of a longitudinal crest on the labial crown shoulder, root vascularization, and overall tooth shape.

The longer, more slender teeth in the sample tend to be those with low coronal profiles. Those teeth with large upright central cusps are often quite deep labio-lingually. Many of the teeth in the sample have heavily eroded central cusps (e.g. P.60671, Pl. 13, fig. 1; Pl. 14, fig. 3) in relation to little worn roots, due largely to ante-mortem wear rather than post-mortem abrasion. Those teeth with well-preserved central cusps often show considerable lingual and distal central cusp inclination (Pl. 14, fig. 9). With progressive lingual inclination of the central cusp, there tends to be a parallel increase in distal inclination of the cusp (see, for example, P.60679, P.60684, P.60688, P.60691, P.60700). Some teeth do show considerable lingual inclination with little distal inclination of the central cusp (P.60676). The basal flange at the labial base of the crown may be prominent in teeth with a high, upright central cusp (P.60670, P.60671), and in teeth with high central cusp inclination (P.60680). The increasing lingual and distal inclination of the central cusp with lowering of the crown profile seems to represent gradient monognathic heterodonty. The development of a strong longitudinal crest along the labial crown shoulder occurs in a few specimens (P.60674, P.60672, Pl. 14, figs. 8, 9).

In the root, the median internal canal may be unroofed in certain cases, although this is probably due to tooth abrasion and transport. P.60696 is unique in that it possesses multiple vascular foramina in the area of the central pit (six foramina lateral to the pit on the single preserved side). Several teeth (P.60675, P.60683, P.60686, P.60687) show one or two lateral foramina along the linguo-basal root border. The lateral vascular canals do not usually exit on the labial root face.

P.60705 has very strong lateral rami developed at the base of the labial root buttress and lateral to the central pit.

Anachronistes sp.

Plate 14, figs. 8, 10

Material. One complete tooth (Pl. 14, figs. 8, 10); Los Angeles County Museum (LACM) catalogue number 119970.

Locality. Ward Mountain, White Pine County, Nevada, U.S.A. Los Angeles County Museum locality 4536.

Lithology. Thinly bedded limestone and calcareous sandstone.

Age. Arcturus Formation, probably *Parafusulina* zone, Leonardian Stage, Early Permian.

EXPLANATION OF PLATE 14

Figs. 1-7, 9. *Anachronistes fordi* from the Lower Carboniferous of England. 1, P.60697 in oblique basal view, $\times 35$. 2, P.60697 in basal view, $\times 30$. 3, P.60671 in lateral view showing labial flange, $\times 50$. 4, P.60690 in basal view, showing medial pit and hemiaulacorhize vascularization, $\times 35$. 5, P.60673 in oblique basal view, $\times 30$. 6, P.60673 in oblique basal view, $\times 30$. 7, P.60672 in lateral view, $\times 35$. 9, P.60672 in labial view, note the cusp inclination and longitudinal crest at the top of the crown shoulder, $\times 30$.
Figs. 8, 10. *Anachronistes* sp. from the Lower Permian of Nevada, U.S.A. 8, LACM 11970 in lateral view, $\times 65$. 10, LACM 11970 in labial view, note the development of lateral cusplets, $\times 60$.



Description. The tooth measures up to 1.1 mm long (mesio-distally). The crown bears a postero-lingually directed central cusp with circular cross-section. The central cusp is flanked by up to two small lateral cusplets on either side (Pl. 14, figs. 8, 10). The occlusal crest is moderate, and runs the length of the crown bisecting the cusp apices. The labial face of the crown possesses a strong basal flange. A longitudinal ridge marks the crest of the labial crown shoulder (Pl. 14, fig. 10). The lingual face of the crown is short and slightly inflated at the base of the central cusp. The crown lacks ornament.

The crown/root junction is deeply incised on the labial side, but smooth on the lingual side. The root projects lingually from the crown undersurface. The labial buttress underlying the basal flange of the crown is well developed (Pl. 14, fig. 8) and gives way lingually to the central pit. The basal face is arched and flat. The root vascularization comprises a median internal canal with a single medio-internal and medio-external entrant foramen.

Remarks. The tooth of *Anachronistes* sp. shows the characteristic basal flange, lateral blade, labial root buttress, and central pit of the genus. The tooth differs from those of *Anachronistes fordii* in the lateral cusplets on the occlusal crest and a longitudinal ridge at the crest of the labial crown shoulder. The tooth certainly belongs to a new species, but is not named here since the currently available material is too sparse to allow adequate definition and diagnosis.

DISCUSSION OF AFFINITIES

The morphology of sharks teeth is very varied and there is no currently accepted analysis of tooth anatomy in phylogenetic terms. For this reason, the individual characters of the tooth anatomy of *Anachronistes* will be considered separately.

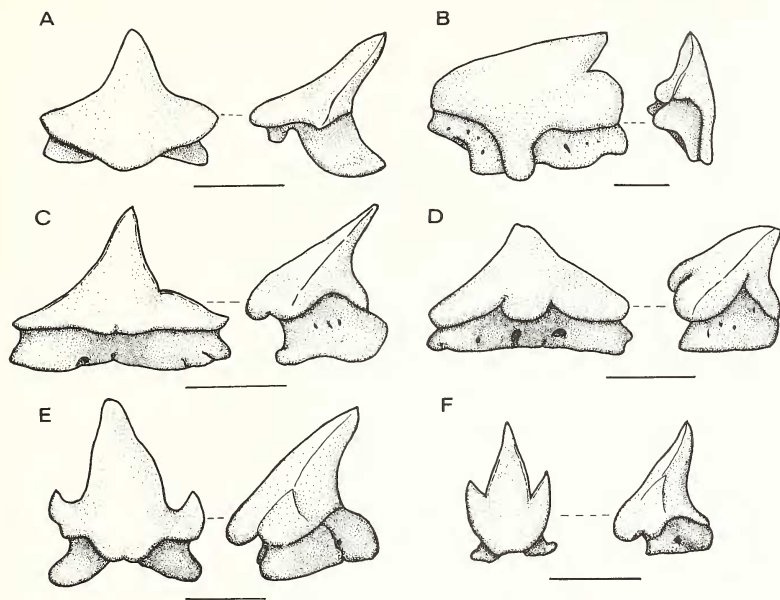
Crown

The teeth of *Anachronistes* possess a crown comprising a conical central cusp flanked by well-developed lateral blades. This is a conservative feature which is variously modified in all four superorders of the Neoselachii to tricuspidate and more complex coronal configurations (Duffin 1980, e.g. Squalomorphii—*Centroscyllium*, *Echinorhinus*; Galeomorphii—*Carcharhinus*, *Odontaspis*, *Brachaelurus*; Squatinomorphii—*Squatina*; Batoidea—*Hypnos*, *Belemnobatis*). Similar morphologies are known in some hybodonts (*Lissodus*, *Hybodus minor*) but are otherwise absent amongst the hybodonts, ctenacanth, xenacanth, and cladoselachians. We believe that the exceptions noted amongst the hybodonts represent convergences with the neoselachian condition since, in other respects, the teeth of these genera are typically hybodont. The conical central cusp flanked by lateral blades is thus probably an apomorphic character of the Neoselachii with respect to the other elasmobranch cohorts, but a plesiomorphic character within the Neoselachii.

There is a labial extension to the base of the crown (basal flange) in the teeth of *Anachronistes* (Pl. 13, figs. 3, 6, 8; Pl. 14, figs. 3, 7, 8; text-fig. 2A). This is a feature found in three of the four superorders of the Neoselachii (Duffin 1980). In the Squalomorphii the labial flange is often plastered on to the labial root face (e.g. *Squalus*, *Oxynotus*, text-fig. 2B), but may be developed as a significant overhang to the crown/root junction, as in *Pristiophorus* and *Pliotrema* (text-fig. 2C, D). In the Galeomorphii, the feature is developed as a labial crown overhang (e.g. *Brachaelurus*, *Stegostoma*, text-fig. 2E, F). In the batoids, the feature is absent, but it is well developed in the Squatinomorphs (*Squatina*). The base of the labial face of the crown is extended in a few hybodonts (*Lissodus*, *Steinbachodus*). In other respects, these genera possess teeth which are typically hybodont; the feature is therefore probably convergent with the neoselachian condition.

Labial root buttress

In the teeth of *Anachronistes* the labial flange development of the crown is supported beneath by a deep labial buttress development of the root (Pl. 13, figs. 1–5, 7, 9; Pl. 14, figs. 1–10). This is flanked medially in basal view by a deep pit which presumably carried blood-vessels to the internal tissues of the crown.



TEXT-FIG. 2. A comparison of the teeth of *Anachronistes* with those of extant neoselachian groups. All teeth are drawn in labial and lateral views. A, *Anachronistes* (BM(NH) P.60670, Lower Carboniferous); B, *Squalus* (Recent); C, *Pristiophorus* (Recent); D, *Pliotrema* (Recent); E, *Brachaelurus* (Recent); F, *Stegostoma* (Recent). Notice that in all cases the crown comprises a conical central cusp flanked by well-developed lateral blades. A prominent basal flange is present in all genera. Bar scale = 1 mm in all diagrams.

The presence of a medial vascular pit and buttressing of the labial flange of the crown is found in only two other genera, to our knowledge: *Squatina* and *Orectolobus* (text-fig. 3). In the teeth of both of these genera the buttressing of the crown is an analogous feature to the condition in *Anachronistes*, since in the former, the root is not directly involved. Instead, the basal flange of the crown is extended basally as a buttress (text-fig. 3A–C). The feature almost certainly arose independently in the Recent and Permo-Carboniferous genera. It may be that the crown modification in the extant genera is more efficient than the condition in *Anachronistes* since it causes less disruption to the vascularization. The function of the labial buttressing of the crown lies presumably in accommodating labially-directed pressure during occlusion, while maintaining a stable tooth row. There is no medial pit in the teeth of Recent *Squatina*. It is present as a possibly variable feature in *Squatina prima* from the English Eocene (text-fig. 3C). In the teeth of this species, multiple vascular foramina are present in the general area occupied by the medial pit in teeth of *Anachronistes* (text-fig. 3D).

In certain species of *Orectolobus* (*O. barbatus*, Recent), the labial buttress is pronounced and the medial pit comprises a single foraminal opening (text-fig. 3B), occasionally carrying several vascular canals.

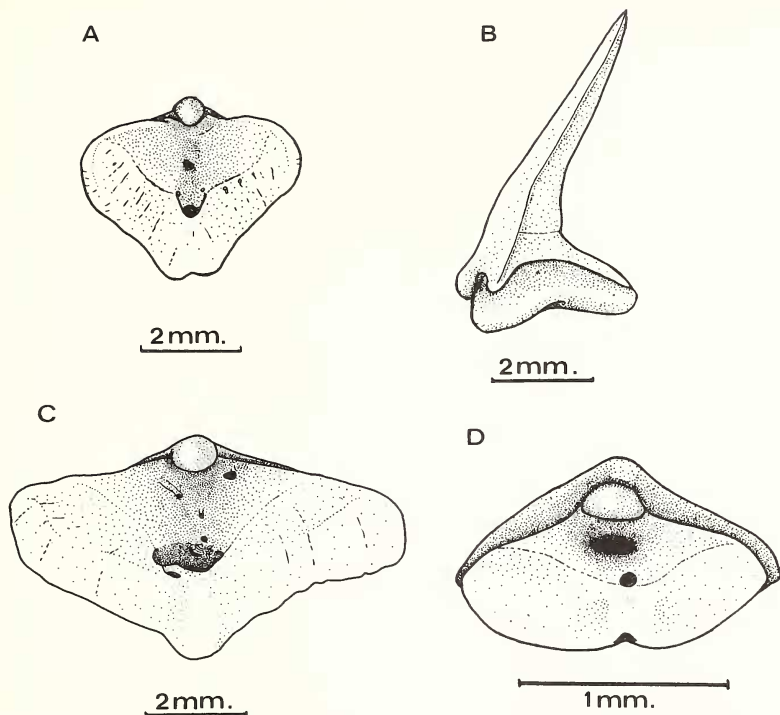
Character Group	Tripartite crown	Labial flange	Labial buttress	Hemiaulacorhize vascularisation	Arcuate root basal face	Central pit	Multiforaminate root	Succession	Heterodonty	Enameloid type
<i>Anachronistes</i>	X	X	X	X	X	X	-	I	?MG	N
Chlamydoselachoids	?	-	-	-	-	-	-	I	MG	T
Hexanchoids	U	-	-	-	-	-	A	A	D, MG	T
Squaliforms	X	X	-	-	X	-	-	A	D, MG	T
Pristiophoriforms	X	X	-	-	X	-	-	Im	MG	?T
Rajiforms	X	-	-	X	X	-	-	I, Im	MG	Ta
Pristiforms	X	-	-	-	X	-	-	Im	MG	?T
Torpediniforms	X	-	-	-	-	-	-	Im	MG	?T
Myliobatiforms	-	-	-	-	-	-	A	Im	MG	?T
Squatiforms	X	X	X	X	X	X	-	I	MG	T
Heterodontiforms	X	-	-	X	X	-	A	Im	MG	T, S
Orectolobiforms	X	X	X	X	X	X	-	Im	MG	T
Lamniforms	X	-	-	-	X	-	-	I	D, MD	T
Carcharhiniforms	X	-	-	X	X	-	-	I, Im	D, MG, MD	T
<i>Palaeospinax</i>	-	-	-	-	-	-	P	Im	MG	T
<i>Pseudodolatias</i>	X	-	-	-	U	-	P	A	D, MG	S
Hybodonts	-	-	-	-	-	-	P	I, A	D, MG	S
Xenacanth	-	-	-	-	-	-	P	I	MG	?N
Ctenacanth	-	-	-	-	-	-	P	I	?MG	S
Cladodonts	-	-	-	-	-	-	P	I	MG	?S

TABLE 1. The distribution of morphological features in the dentitions of Recent and fossil selachians. X, feature present; —, feature absent; ?, feature may be present; U, feature present in upper dentition only. Multiforaminate root vascularization: A, feature present and considered to be advanced; P, feature present but considered to be primitive. Tooth succession: I, teeth arranged in independent tooth rows; Im, adjacent tooth rows show imbrication; A, adjacent tooth rows alternate. Heterodonty: D, dignathic heterodonty; MG, monognathic gradient heterodonty; MD, monognathic disjunct heterodonty. Enameloid: T, triple-layered; S, single crystallite; N, no enameloid; Ta, tangled fibre enameloid. (Data compiled from Reif 1973, 1974, 1977, 1978; Duffin 1980.)

Vascularization of the root

Casier (1947a-c) introduced a series of terms for the vascularization patterns found in the roots of extant and fossil sharks teeth (text-fig. 4). He considered that the multiforaminate condition so typical of hybodonts was ancestral to the reduced vascularization of most neoselachians. The multiforaminate teeth he termed 'anaulacorhize' (text-fig. 4A); those teeth possessing a partially covered median root canal he termed 'hemiaulacorhize' (text-fig. 4B), and those with an open median root canal he termed 'holaulacorhize' (text-fig. 4C). The condition with multiple open root canals, as seen in the myliobatiforms, he termed 'polyaulacorhize' (text-fig. 4D). He saw the development of these vascularization types in phylogenetic terms as the sequence anaulacorhize-hemiaulacorhize-holaulacorhize-polyaulacorhize, assuming that the hybodonts were a basal stock.

Casier (1947c, fig. 1, p. 3) considered that by suppression of entrant vascular foramina, the central cavity within the hybodont root diminished in size, now being fed by a series of labio-lingual internal canals, to become a root of *Synechodus*/*Palaeospinax* appearance. The median, and certain lateral



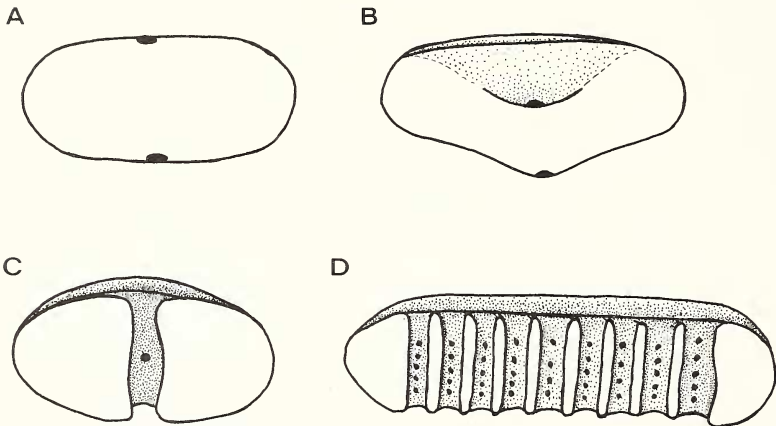
TEXT-FIG. 3. Labial buttressing and the presence of the medial pit in sharks' teeth. A, tooth of *Orectolobus barbatus* (Recent) in basal view. Note the extension of the labial flange to provide a buttress on the labial side of the root, and the presence of a medial pit. B, *O. barbatus* in oblique lateral view. C, tooth of *Squatina prima* (English Eocene) in basal view. Note the labial flange development as a buttress, and the presence of vascular foramina in the area occupied by the medial pit in other genera. D, tooth of *Anachronistes* (BM(NH) P.60673) in basal view.

Labial buttressing is provided by a special feature of the root, flanked lingually by a deep medial pit.

internal vascular canals were retained during transformation to a *Squatina* root type, with an enlarged medio-internal foramen at which the median internal canal and central cavity were exposed. There were then two possible evolutionary pathways, according to Casier; elimination of the central cavity together with loss of the roof of the median canal produced roots of *Rhynchobatus* type; enclosing the opening of the central cavity, with its subsequent constriction, within the unroofed median internal canal produced roots of the *Ginglymostoma* and *Scyliorhinus* types.

The hybodont origin of the neoselachians is no longer accepted (Maisey 1975; Herman 1975; Compagno 1973, 1977; Reif 1977, 1978; Duffin 1980). Anaulacorhize vascularization is not restricted to the hybodonts, however, because Recent *Chlamydoselachus*, hexanchoids and squaloids, as well as

some Jurassic scyliorhinids and rhinobatids also show this feature. There is no evidence from the fossil record in support of Casiers hypothetical transition from an anaulacorhize, through an hemiaulacorhize to an holaulacorhize vascularization. It is more probable that the vascularization progressed directly from an anaulacorhize to an holaulacorhize condition by loss of the floor of the medio-internal canal (text-fig. 5). The hemiaulacorhize condition is seen in the teeth of *Squatina*, some orectolobids, the anterior teeth of *Heterodontus*, and in *Anachronistes*. The former three groups are mostly specialized benthonic sharks that stabilized in the Middle to Upper Jurassic. It would seem that the hemiaulacorhize condition is a specialization related to bottom feeding habits.



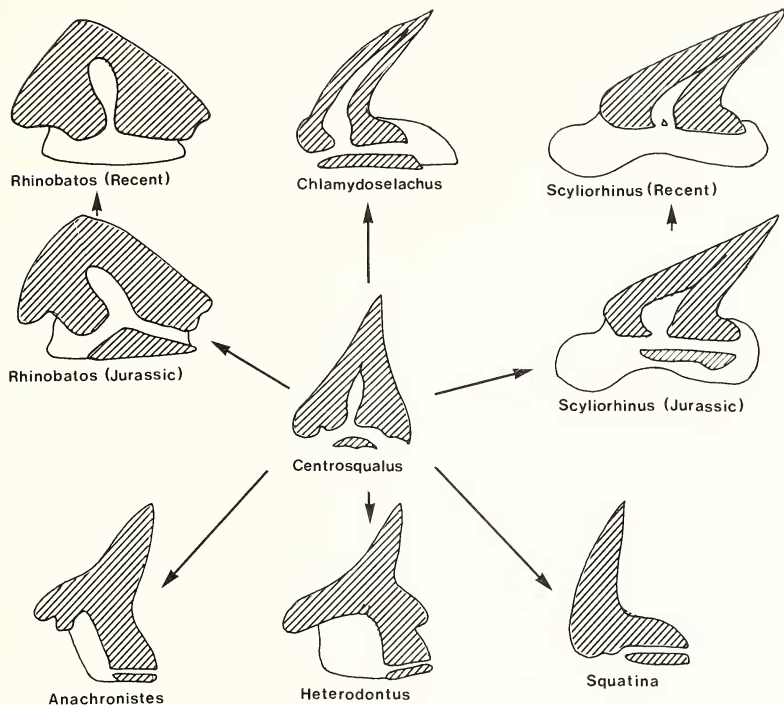
TEXT-FIG. 4. Vascularization patterns in Recent and fossil sharks teeth. All teeth are in basal view (after Casier 1947c). A, anaulacorhize vascularization; B, hemiaulacorhize vascularization; C, holaulacorhize vascularization; D, polyaulacorhize vascularization. Casier visualized these vascularization types as a progression, A-D.

Basal face of the root

Duffin (1980) suggested that the arcuate or V-shaped basal root face is typical of neoselachians belonging to the superorders Squalomorphii, Squatinomorphii (text-fig. 4C), and Galeomorphii (text-fig. 4A). It is probably a synapomorphic character of these groups (Table 1). The teeth of *Anachronistes* possess a gently arcuate basal root face in which the apex is directed lingually and the lateral wings are directed labially (see Pl. 14, figs. 2, 4-6; text-fig. 3D).

Tooth succession

The teeth of *Anachronistes* may have been arranged in distinct tooth rows with no overlap of the lateral blades of teeth in adjacent rows (as in *Squatina*, xenacanth, ctenacanth, cladodonts, carcharhiniforms, chlamydoselachoids, and certain rajiforms, hybodonts, and lamnoids—Table 1). Alternatively there may have been some overlap between the lateral blades of teeth in successive tooth rows (imbricate tooth succession, Strasburg 1963) as in pristiophoriforms, pristiforms, torpediniforms, myliobatiforms, heterodontiforms, *Palaeospinax*, orectolobiforms, and certain rajiforms and carcharhiniforms (Table 1). The teeth of one row would not have articulated with those of adjacent tooth rows (as in hexanchoids, squaliforms, *Pseudodalatias*, and certain ?hybodonts—Table 1) since no mesial or distal articular facets are developed on either the root or the crown in *Anachronistes*.



TEXT-FIG. 5. Diagram to show the hemiaulacorhize vascularization in sectioned teeth of various Recent and fossil neoselachians. Morphometric changes from a typical anaulacorhize tooth (*Centrosqualus*) to hemiaulacorhize conditions in various neoselachian lineages. No direct evolutionary relationship is inferred.

Tooth succession does not appear to be a useful taxonomic feature amongst the selachians so far as can be judged at the present time.

Heterodonty

Applegate (1967) identified two types of heterodonty in shark dentitions. The first he termed dignathic heterodonty, involving differences in morphology in those teeth found in corresponding positions in opposite jaws. Monognathic heterodonty involves differences between teeth in different position in the same jaw. There are two types of monognathic heterodonty: gradient monognathic heterodonty involves gradual change in coronal profile of teeth along the length of the jaw; disjunct monognathic heterodonty involves marked dissimilarities between adjacent teeth in the same jaw. Compagno (1970, p. 73) added two further heterodonty types to this list—ontogenetic heterodonty and gynandric (sexual) heterodonty, which are self-explanatory.

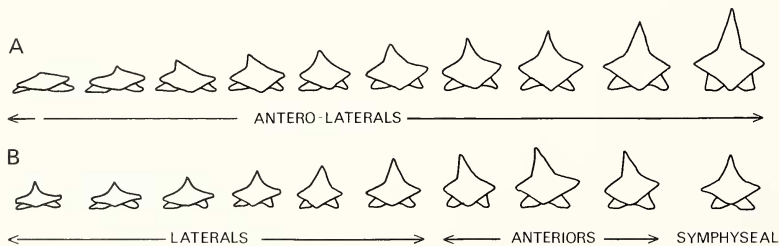
The teeth of *Anachronistes* presently available, show mild gradient monognathic heterodonty. There is no positive evidence for dignathic, gynandric, or ontogenetic heterodonty in the teeth of *Anachronistes*. Monognathic heterodonty is common to all known shark orders (but not to every genus) (Table 1), and so heterodonty is not presently useful as a taxonomic feature, so far as the teeth of *Anachronistes* are concerned.

The usual form of monognathic gradient heterodonty in shark dentitions involves decrease in crown height, increase in mesio-distal width of the crown base, increase in size and number of lateral cusplets or increase in size of lateral blades, and increase in lingual inclination of the central cusp, from teeth in the symphyseal position to those in the commissural position. This basic pattern is found in the Recent genus *Orectolobus*, and is here designated linear gradient monognathic heterodonty. In teeth of Recent *Squatina*, however, there is a general increase in crown height to the fourth distal tooth row, and then a gradual lowering of the crown profile distally. Also, the distal inclination of the central cusp appears to increase symphyseally, and the teeth of the parasymphyseal tooth row possess an almost upright crown. The lateral blade development follows that of linear gradient heterodonty. The pattern of heterodonty shown by the teeth of Recent *Squatina* is here designated non-linear gradient monognathic heterodonty. This type of heterodonty is particularly well developed in the batoids, such as *Rhynchobatus*, *Rhina*, and some species of *Dasyatis*. It is also present in modified form in dentitions of the hybodonts *Acrodus* and *Asteracanthus* (see, for example, Reif 1976, fig. 39), and appears to be an adaptation for durophagous diet.

The samples of teeth of *Anachronistes* presently available are insufficient to judge from the type of gradient monognathic heterodonty it displays. Indeed, the teeth of *Anachronistes* can be equally well arranged to show linear or non-linear gradient monognathic heterodonty (text-fig. 6). The point to be made from the distinction between the two types of heterodonty is that a high-crowned tooth is not necessarily a mesial tooth.

Enameloid ultrastructure

There has been some debate over the tissue covering the crown in sharks teeth. It has been variously identified as true enamel (i.e. ectodermal in origin) and as enameloid (mesodermal in origin) (Applegate 1967; Moss 1977). The tissue will be here referred to as enameloid. Reif (1973, etc.) has found that hybodont and ctenacanth teeth possess a single crystallite enameloid, the individual crystallites of which have no preferred orientation (e.g. Reif 1978, fig. 7a, b). Neoselachian teeth, on the other hand, possess a triple-layered enameloid comprising a basal enameloid of tangled fibres, a middle enameloid of parallel fibres, and a surface layer of shiny enameloid (Table 1). Reif (1978, p. 53) states that this enameloid type is known in all living sharks and fossil neoselachian sharks. He even uses enameloid ultrastructure to define genera (Reif 1977). There is a discrepancy within the



TEXT-FIG. 6. Possible reconstructions of the dentition of *Anachronistes* showing A, linear gradient monognathic heterodonty, B, non-linear gradient monognathic heterodonty.

enameloid of the teeth of *Heterodontus*. Reif (1977) notes that mesial teeth of *Heterodontus* possess a triple-layered enameloid, but that distal crushing teeth possess a single crystallite enameloid as in the hybodonts, covered by a thick layer of tangled fibre enameloid. Reif (1977, p. 572) interprets the presence of a single crystallite enameloid in lateral teeth of *Heterodontus* as being a convergence with the hybodonts and ctenacanth in order to meet the high pressure stresses set up in the teeth during crushing of food. Bearing the teeth of *Heterodontus* in mind, it might be better to state that triple-layered enameloid indicates neoselachian affinity, but that the converse is not true. The lack of triple-layered enameloid does not necessarily exclude neoselachian affinity, and neither does it therefore positively indicate hybodont or ctenacanth affinity.

One tooth of *Anachronistes fordii* (P.60674) and one tooth of *Anachronistes* sp. was etched in 2N HCl for 3 seconds, dried, covered with a 50 Å thick coating of evaporated gold, and studied using a Cambridge Stereoscan 600 microscope, using an acceleration voltage of 15 kV.

The teeth of *Anachronistes* possess no enameloid layer; the surface of the crown and the occlusal crest appears to comprise compact osteodentine. In our opinion, the lack of enameloid in teeth from Britain and the United States is not due to post-mortem wear. Other teeth in the Steeplehouse Quarry sample possess well-defined enameloid. Neither does the lack of enameloid represent excessive etching since the prepared specimens show sharply defined features (Pl. 14, fig. 10).

Enamel and enameloid have arisen independently in different vertebrate groups. It would not seem unreasonable to suppose that this might be true within the Chondrichthyes. *Anachronistes* could represent a condition pre-dating enameloid acquisition in the neoselachins. Alternatively, *Anachronistes* may have lost enameloid as a secondary feature.

Finally, it should be noted that the tooth form of *Anachronistes* is easily distinguished from that of contemporary petalodonts. The latter possess teeth which are distinct in possessing labio-lingually compressed and scallop-shaped crowns which possess longitudinal ridges basally. The occlusal crest is often serrated or denticulate, and the crown contains 'tubular' dentine.

The tooth shape of *Anachronistes* is probably adapted to bottom feeding. Further evidence in favour of durophagous diet is the nature of the ante-mortem coronal wear. The shark may well have been dorso-ventrally flattened with large pectoral fins as in the Recent Wobbegong (*Orectolobus*) and Angel Shark (*Squatina*). This body form is not without precedent in the Palaeozoic. Lund and Zangerl (1974) describe *Squatina caudispinatus* from the Upper Mississippian of Montana. This shark possesses a roughly squatinoid body form together with multicuspoid cladodont teeth.

It is also interesting to note here that Zidek (1976) implies the presence of neoselachian sharks in the Carboniferous with the description of an egg capsule named *Palaeoxyris lewisi* from the Pennsylvanian of Oklahoma. Zidek concludes that the Palaeozoic egg capsule shows the closest affinity with egg capsules of *Heterodontus*.

PALAEOECOLOGY

The teeth of *Anachronistes* from Steeplehouse Quarry were found in association with presently undetermined xenacanth, petalodont, palaeoniscid, and *Cladodus* teeth, hybodont teeth and dermal denticles, placoid scales, palaeoniscid scales and vertebrae, and internal casts of textulariid foraminifera (Dr. J. E. Robinson, pers. comm.). The most abundant component of the fauna is the scales of *Petrolodus patelliformis* M'Coy (1848) (Ford 1964). The associated invertebrate fauna, as given by Ford (1964, p. 4), comprises the corals *Dibunophyllum bipartitum* M'Coy, *Caninia juddi* (Thomson), *Zaphrentis* spp., *Michelinia tenuisepta* (Phillips), *Emmonsia parasitica* (Phillips), and *Chaetetes septosus* (Fleming); the brachiopods *Echinoconchus punctatus* (J. Sowerby), *Pustula putulosus* (Phillips), *Gigantoproductus giganteus* (J. Sowerby), *Dictyoclostus semireticulatus* (Martin), *Athyris* sp. and *Spirifer bisulcatus* J. de C. Sowerby; numerous bryozoans; and crinoid ossicles.

The associated fauna from Esclusham Mountain is similar to that of Steeplehouse Quarry with regard to the vertebrates, although the quantitative species representation is very different. The vertebrate faunas will be described in detail in a later paper (Duffin, in prep.). Dr. B. Rosen is preparing an account of the coral associations from Esclusham Mountain.

Ford (1964) concludes that the bed yielding *Anachronistes* at Steeplehouse Quarry was deposited in an off-reef area. He concludes that the bed comprises locally derived material which was rapidly deposited, perhaps as a result of an inter-reef scour and subsequent deposition in quieter off-reef waters. Certainly, good biohermal reefs, fore-reef and inter-reef facies, together with lagoonal deposits are known from Steeplehouse Quarry and adjacent quarries in the Coal Hills complex of Wirksworth (Ford 1980; Shirley 1959). The presence of xenacanth shark teeth as part of the faunal association may indicate that certain faunal elements were not indigenous to the broad reef complex, but transported into the area from freshwater areas, possibly lagoons.

CONCLUSIONS

From the above discussion we feel it reasonable to conclude that *Anachronistes* is a neoselachian shark because it possesses a conical central cusp, well-developed lateral blades and a basal flange, a V-shaped basal face to the root, and typical neoselachian root vascularization (hemiaulacorrhize).

Anachronistes possesses several characters which are shared by teeth of *Squatina* and *Orectolobus*. These features are the labial buttress on the underside of the labial flange, and the central vascular pit on the root. The complex of characters shown by *Anachronistes* is most closely paralleled in *Squatina* and *Orectolobus*. Both of these genera belong to relatively primitive neoselachian groups, and are coincidentally among the earliest known Jurassic neoselachians. It is unlikely that *Anachronistes* is a stem neoselachian since it is adapted to the specialized habit of a bottom feeder.

The gross morphology of sharks teeth remains a useful taxonomic tool. Two new terms are introduced concerning monognathic heterodonty in shark dentitions. Linear gradient monognathic heterodonty is that in which there is gradual reduction in coronal profile of teeth commissurally (e.g. *Orectolobus*), while non-linear gradient heterodonty involves the presence of high-crowned teeth part way along the jaw, and then subsequent lowering of the coronal profile mesially and distally (e.g. *Squatina*).

The early record of the neoselachians is thus established as extending into the Lower Carboniferous of Britain and the Lower Permian of the U.S.A. It is expected that the Carboniferous record of the neoselachians will prove to be quite diverse, and that the neoselachian lineage is as old as that of the hybodonts, and possibly the ctenacanth and cladoselachians.

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